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Physiology of Ecotypic Plant Response to Sulfur Dioxide in 'Geranium carolinianum' L

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16. ABSTRACT

Populations of Geranium carolinianum, winter annual plant common in disturbed habitats vary in their folair response to sulfur dioxide and pollution resistance is characteristic of populations sampled from areas in which SO_2 has been a prominent stress. The physiological basis of this ecotypic response was investigated using a whole-plant gaseous exchange system in which leaf resistance to H_2O efflux and SO_2 influx were concurrently monitored. Individual plants of distinct SO2 susceptibility were exposed to pollutant concentrations of either 0.4, 0.6, or 0.8 ul^{-1} in both the dark and light. Total SO_2 flux ($ug\ cm^{-2}\ h^{-1}$) to the plant which is the sum of leaf adsorptive and absorptive loss, varied as an inverse function of leaf resistance ($s\ cm^{-1}$), and the relationship was modeled using linear regression techniques. Total SO_2 flux was partitioned to leaf surface and internal fractions using estimation procedures with the regression analysis. SO_2 flux into the leaf interior, the pollutant fraction responsible for causing foliar injury, was strikinly similar for resistant and sensitive plants at each concentration. Resistant plants must absorb 30 percent more SO_2 than their sensitive counterparts in order to exhivit comparable levels of foliar injury. Therefore, in G. carolinianum the predominant explanation for genetically controlled and quantitatively inherited differences in plant response to SO_2 is not variable pollutant flux but rather disparate physiological-biochemical processes affecting pollutant toxicity, cellular perturbation and repair.

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Physiology of Ecotypic Plant Response to Sulfur Dioxide in *Geranium carolinianum* L.

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Summary. Populations of *Geranium carolinianum*, a winter annual plant common in disturbed habitats, vary in their foliar response to sulfur dioxide, and pollution resistance is characteristic of populations sampled from areas in which SO_2 has been a prominent stress. The physiological basis of this ecotypic response was investigated using a whole-plant gaseous exchange system in which leaf resistance to H_2O efflux and SO_2 influx were concurrently monitored. Individual plants of distinct SO_2 susceptibility were exposed to pollutant concentrations of either 0.4, 0.6 or 0.8 µl l^{-1} in both the dark and light. Total SO_2 flux (µg cm^{-2} h^{-1}) to the plant, which is the sum of leaf adsorptive and absorptive loss, varied as an inverse function of leaf resistance (s cm^{-1}), and the relationship was modeled using linear regression techniques. Total SO_2 flux was partitioned to leaf surface and internal fractions using estimation procedures with the regression analysis. SO_2 flux into the leaf interior, the pollutant fraction responsible for causing foliar injury, was strikingly similar for resistant and sensitive plants at each concentration. Resistant plants must absorb 30% more SO_2 than their sensitive counterparts in order to exhibit comparable levels of foliar injury. Therefore, in *G. carolinianum* the predominant explanation for genetically controlled and quantitatively inherited differences in plant response to SO_2 is not variable pollutant flux but rather disparate physiological-biochemical processes affecting pollutant toxicity, cellular perturbation and repair. This conclusion is relevant to understanding how populations of *G. carolinianum* respond over time to elevated levels of SO_2 and may explain the inherent susceptibility of this species compared with plants with which it co-exists.

Introduction

Air pollution is increasingly common as an ecologically important component of the environment. Ozone, sulfur dioxide, nitrogen oxides and acidic precipitation, occurring singly or in combination, are no longer solely localized atmospheric phenomena. One consequence of polluted air being a prominent long-term environmental stress is that plants in affected regions may exhibit specific morphological and physiological attributes that enhance survival and reproduction in the polluted atmospheres. These traits arise through either an induced modification of the phenotype (plasticity response) or a change in the populations's gene pool (ecotypic differentiation). In the former case, the capacity to respond in a comparable manner is common throughout the species, whereas in the latter greater pollution resistance at the infraspecific level would be characteristic only of populations thriving in areas experiencing pollution stress.

The evolution of resistant populations (ecotypes) to air pollution is reported in several plant species. In an analysis of variable responses in *Lupinus bicolor* subspecies to ambient air in the Los Angeles Basin, Dunn (1959) found that subspecies from the basin exhibited less foliar injury than their counterparts from non-polluted locations. He hypothesized that greater smog resistance of the L.A. Basin plants arose through the process of natural selection. Similar examples of ecotypic population responses to air pollution are reported for population growth and survival in *Calluna vulgaris* (Sokolowski 1976), enzymatic reactions in *Rumex obtusifolius* (Horsman and Wellburn 1977), yield responses in *Lolium perenne* (Bell and Clough 1973; Horsman et al. 1979) and reproductive success in *Lepidium virginicum* (Murdy 1979). Although several reports (Catcheside 1975; Gressel and Segel 1978) concluded that microevolutionary plant responses to chemical residues of anthropogenic origin are unlikely, it appears that genetic adaptation may be a common response of plant populations in habitats experiencing elevated levels of atmospheric pollutants.

One example of genetic adaptation in response to air pollution is the evolution of SO_2 resistance within populations of *Geranium carolinianum* L. inhabiting a region experiencing variable SO_2 stress for a maximum of 31 years (Taylor and Murdy 1975). In a comparison of the SO_2 response of eight different populations of this species that were exposed to SO_2 under controlled conditions, those sampled from SO_2 stressed locations were more resistant to acute foliar injury than their counterparts from non-polluted sites. Consistent differences in SO_2 response between individuals of this species are genetically controlled and quantitatively inherited (Taylor 1978a). Initial investigations (Taylor 1976) reported no difference among *G. carolinianum* plants in their stomatal resistance to H_2O flux in both ambient and SO_2-polluted atmospheres. These data, specific for H_2O efflux, support the hypothesis that pollutant uptake is equivalent between individuals; however, it assumes that SO_2 and H_2O experience comparable source-to-sink resistances and concentration gradients. This may not be valid, particularly in light of the residual resistance component associated with CO_2 assimilation but not H_2O efflux (Gaastra 1959; Nobel 1974; Meidner 1975). An analogous residual resistance may affect the influx of SO_2 (Mansfield 1973; Barton et al. 1980). Therefore, experiments to assess the uptake of SO_2 in resistant and sensitive plants were conducted to investigate how genotypic differences effect changes in a plant's physiological state so that plant-to-plant variation exists.

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IV. Discussion

It is evident from this study that the Santa Fe *Bursera graveolens* are recovering from near extinction, and that seed dispersal by animals is playing an important role in the recovery process. Although the cause(s) remains unknown, regeneration of *Bursera* is inhibited under adult trees. Thus dispersers, by carrying seeds away from parent *Bursera*, are effecting a more rapid increase in the species' population than would otherwise be possible.

Each juvenile *Bursera* represents both successful seed dispersal and success in establishment. Specific "safe site" requirements for germination and growth may result in mortality of many "incorrectly" dispersed seeds; to the extent that this is true, the observed distribution of juveniles reflects only a portion of the dispersal of *Bursera* seeds by animals. No data exist on either the proportional input of seeds to specific microhabitats, or on survival rates within these sites. Nevertheless our data demonstrate that establishment is at least possible in several gross substrate types, as well as both under and away from other woody plants.

The association between *Bursera* juveniles and *Opuntia* trees could be due either to attraction of *Bursera* dispersers to the *Opuntia* or to favorable conditions for establishment at the base of the cactus trees. When information is gathered on the identity and behavior of the animals actually dispersing *Bursera* seeds, this relationship can be unraveled. In any case the *Opuntia*/*Bursera* association demonstrates that the distribution of juveniles results from an interplay between biotic factors and the distance from source trees.

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Materials and Methods

Plant uptake of SO_2 was investigated using an open gas-exchange system (Tingey et al. 1979; Taylor and Tingey 1979) operating on the mass balance principle. The chamber, which enclosed the above-ground portion of the plant, was housed within a controlled environmental unit. To assess gaseous fluxes, air flow rates and concentrations of SO_2 and H_2O vapor were measured at the chamber's inlet and outlet. Within the chamber, rapid air mixing was maintained by wall baffles and impeller blades rotated by an externally-mounted electric motor. Fan speed maintained as slight, uniform flutter among all leaves of the plant. The boundary layer resistance of the leaves to H_2O efflux was calculated using an energy budget approach (Sestak et al. 1971) and was consistently low at 0.2 s cm^{-1}. All gas lines were stainless steel and heated after leaving the chamber to prevent in-line condensation.

From seed sampled from native populations of *G. carolinianum*, selection has been successful in establishing lines of varying SO_2 resistance. This variation is genetically controlled and quantitatively inherited (Taylor 1978a). Each line continues to exhibit variation in SO_2 response although the mean, mode and limits of resistance differ among lines. Seed from sensitive and resistant lines was germinated and seedlings were grown in a Jiffy Mix:Perlite (1:2; V:V) mixture. Plants were cultured initially in a greenhouse with maximum day/night temperatures of 28° C and 20° C, respectively. The photoperiod was extended to 16 h per day with HID sodium vapor lamps. A modified Hoaglands nutrient solution (Downs and Hellmers 1975) was applied daily. At least two weeks prior to experimentation, plants were transferred to a controlled environmental unit with a regime similar to that of the gas-exchange chamber. Within the gas-exchange system, the chamber's air and outlet dew point temperatures were maintained at 27° C and 23° C, respectively (chamber humidity levels of 70–75%); these temperatures were selected to mimic the late spring climatic conditions typical of the Piedmont region of the southeastern United States where the original populations were sampled. Daylight irradiance at canopy level and air temperature were 490 μE m^{-2} s^{-1} and 25° C, respectively; leaf temperature was measured with a fine wire thermocouple (Lange 1965) and was 28° C ± 1° C. Outlet CO_2 concentration was 345 ppm ± 20 ppm.

In using the mass balance approach to analyze the rate of gaseous exchange, the fate of SO_2 molecules entering the chamber must be assessed. These include (1) reaction with the plant, (2) adherence to the chamber walls, and (3) exiting the chamber unreacted; the last is the ambient concentration to which the plants were exposed. The magnitude of the chamber surfaces as a sink for SO_2 is a function of the construction material and H_2O content of the air. To determine the SO_2 sink capacity of the chamber surfaces, humid air was injected into the chamber to elevate the outlet dew point to levels similar to those created by the plants. The adsorption of SO_2 to chamber surfaces increased linearly with dew point (SO_2 loss = 2.42 dew $point_{outlet}$ − 26.32, $r = +0.985$). The data indicate that when outlet dew point levels exceed 20° C (70% R.H.), 20% of the SO_2 entering the chamber is adsorbed to the chamber. This equation was incorporated in all analyses to determine more accurately how much of the SO_2 entering the chamber reacted solely with the plant.

Total flux of SO_2 to the plant (J_T) is the sum of pollutant loss to the leaf surface (adsorption or J_s) and leaf interior (absorption or J_i). Estimates of J_s were determined from pollutant flux in the dark, while J_T was derived from flux in the light. Estimates of J_i were calculated by subtraction (i.e., $J_i = J_T - J_s$). The objective was to establish concurrent and steady-state values for the flux of H_2O and SO_2 in atmospheres containing 0.4, 0.6, or 0.8 μl·l^{-1} SO_2 in the dark and light, respectively. Constant flux values were typically attained within an hour in both dark and light, but measurements continued for an additional 3 h. The duration of exposure in the light was 4 h. The low level SO_2 dose (0.4 μl·l^{-1}) did not elicit any leaf injury, whereas the intermediate and high doses caused slight (0–5%) and moderate (20–40%) leaf necrosis, respectively, on SO_2-sensitive individuals only. Leaf blades were removed and leaf area (one side only) measured after terminating exposure. Values for SO_2 flux to the plant (μg cm^{-2} h^{-1}) and leaf resistance to H_2O flux (s cm^{-1}) at one-half hour intervals in both the dark and light were calculated. Total leaf resistance to H_2O efflux was used to determine the value for resistance to SO_2 flux. This calculation assumes that resistance to SO_2 diffusion through the boundary layer and stomate is equivalent to that for H_2O, taking into account the differences in the diffusivity in air of the two gases (Nobel 1974; Unsworth et al. 1976).

Results

An example of the patterns of leaf resistance to gaseous flux ($R_L^{H_2O}$ and $R_L^{SO_2}$) and pollutant flux to the plant over the dark to light regime at 0.4 μl·l^{-1} SO_2 is shown in Fig. 1; the patterns were similar for all SO_2 exposure concentrations. In the dark, leaf resistance was high (17 and 32 s cm^{-1} for $R_L^{H_2O}$ and $R_L^{SO_2}$, respectively); with light, resistance decreased within an hour to an 83% lower steady state value. The flux of SO_2 to the plant exhibited distinctly different dark and light steady state values, and the pattern is the reverse of that recorded for leaf resistance. Pollutant flux was lowest in the dark (0.8 μg cm^{-2} h^{-1}) and increased rapidly with light. The light-associated flux (2.5 μg cm^{-2} h^{-1}) was 3 times that observed in the dark. SO_2 flux in the dark represents pollutant adsorption to the leaf surface (J_s) while that observed in the light is total flux (J_T) or adsorption plus absorption.

Concurrent steady state measures of leaf resistance ($R_L^{H_2O}$ and $R_L^{SO_2}$) and SO_2 flux at 0.4 μl·l^{-1} SO_2 were collated for night and day conditions within SO_2 resistant and sensitive plants (Fig. 2). SO_2 flux (J_T) was inversely related to leaf resistance.

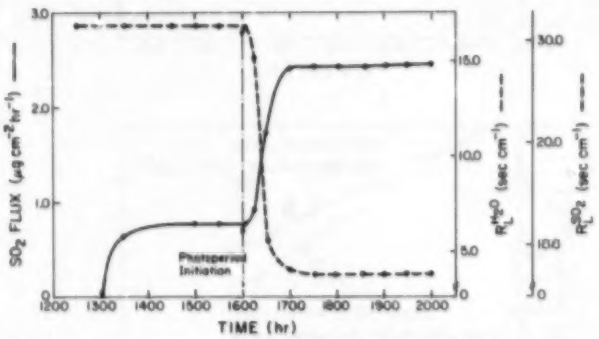

Fig. 1. Concurrent values for SO_2 flux and leaf resistance ($R_L^{H_2O}$) before and after photoperiod initiation and at a constant SO_2 atmospheric level of 0.4 μl·l^{-1}

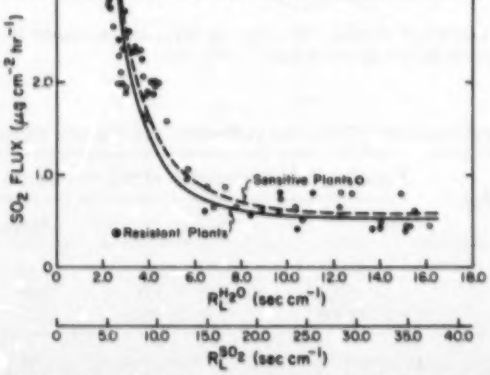

Fig. 2. Flux of SO_2 as a function of leaf resistance to gaseous flux at SO_2 concentration of 0.4 μl·l^{-1}

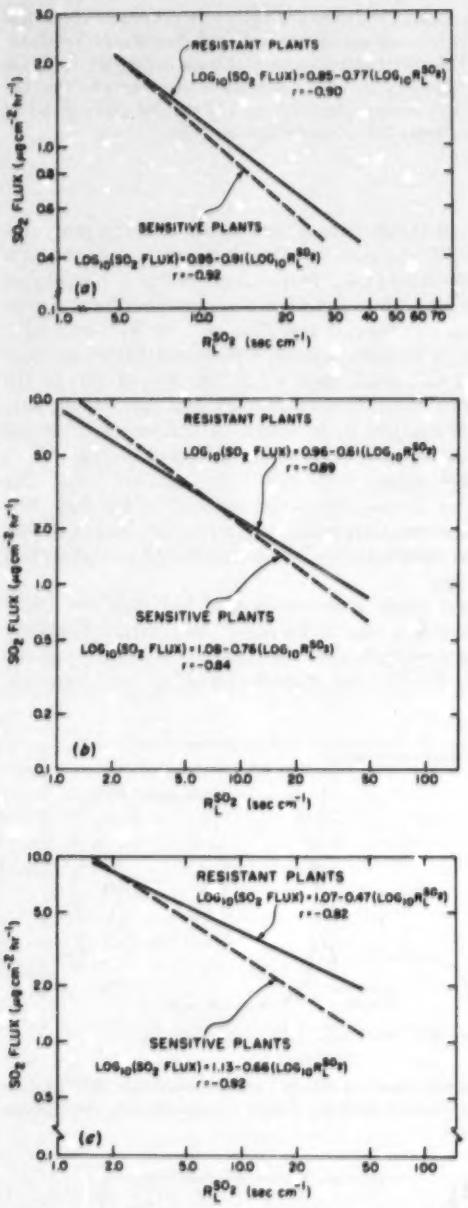

Fig. 3. Regression of the $\log_{10}$ SO_2 flux on $\log_{10}$ leaf resistance to SO_2 flux at 0.4 (**a**), 0.6 (**b**) and 0.8 $\mu l \cdot l^{-1}$ SO_2 (**c**)

At leaf resistances above $R_L^{H_2O} = 10$ s cm^{-1}, pollutant flux remained essentially constant. In contrast, at low leaf resistances ($R_L^{H_2O} \leq 4$ s cm^{-1}) rapid increases in SO_2 flux were associated with small changes in leaf resistance to gaseous flux. Between these two extremes, SO_2 flux exhibited characteristics of exponential decay with increasing resistance.

This relationship between total SO_2 flux and leaf resistance was modeled for both resistant and sensitive plants using linear regression analysis of the $\log_{10}$ transformed values for each variable (Fig. 3a). For resistant and sensitive plants the slopes and Y-intercept values were not statistically different, indicating that SO_2 flux as a function of leaf resistance at a concentration of 0.4 $\mu l \cdot l^{-1}$ could be described by a common regression line. Therefore, at this concentration leaf flux of SO_2 is similar for plants of *G. carolinianum* that vary in their inherent susceptibility to the pollutant.

At 0.6 $\mu l \cdot l^{-1}$ SO_2 a comparable pattern of decreasing pollutant flux with increasing leaf resistance was recorded, and the linear regression model of the $\log_{10}$ transformed variables for resistant and sensitive plants is shown in Fig. 3b. A common regression line statistically describes the relationship of leaf resistance and SO_2 flux in resistant and sensitive plants. Consequently, the flux of SO_2 at this concentration is similar for plants that vary intrinsically in their SO_2 susceptibility. At 0.8 $\mu l \cdot l^{-1}$ SO_2, the relationship between R_L and SO_2 flux is similar to that recorded at the lower concentrations, i.e., the model accounts for approximately 90% of the variation. However, unlike the previous examples, the responses of resistant and sensitive plants can not be modeled by a common regression line (Fig. 3c). Even though the two regression lines intersect at a low leaf resistance (2.0 s cm^{-1}), the statistically different slopes result in a lower SO_2 flux to sensitive plants at high leaf resistance values.

SO_2 uptake was partitioned into internal (J_I) and surface (J_S) fractions at each concentration for resistant and sensitive plants by estimating total (J_T) flux at the same leaf resistance value in the light ($R_L^{SO_2} = 6$ s cm^{-1}); the corresponding estimate at high leaf resistance ($R_L^{SO_2} = 19$ s cm^{-1}) represented J_S. The J_I fraction was calculated by subtraction, and these data are recorded in Table 1. Except for one instance (0.8 $\mu l \cdot l^{-1}$ SO_2 in resistant plants), J_I is larger than J_S and ranged from 42–66% of J_T. The relative importance of each fraction varies with concentration (Fig. 4). In both resistant and sensitive plants, progressively less SO_2 (on a relative basis) is absorbed into the leaf interior with increasing pollutant concentration. Although this pattern is observed in both groups, the response is consistently displaced about 10% higher for sensitive plants.

This relative decrease in the importance of J_I with increasing ambient SO_2 concentration does not mean less absolute pollutant flux into the leaf interior (Fig. 5). As SO_2 concentration rose

Table 1. Leaf Fractions[a] of SO_2 Flux in Resistant and Sensitive Plants at Three SO_2 Concentrations

SO_2 concentration $\mu l \cdot l^{-1}$	Resistant plants leaf fractions of SO_2 flux ($\mu g \cdot cm^{-2} \cdot h^{-1}$)			Sensitive plants leaf fractions of SO_2 flux ($\mu g \cdot cm^{-2} \cdot h^{-1}$)		
	J_{Total}	$J_{Surface}$	$J_{Internal}$	J_{Total}	$J_{Surface}$	$J_{Internal}$
0.4	1.85 (1.15)	0.75 (1.09)	1.11	1.83 (1.17)	0.62 (1.13)	1.21
0.6	3.23 (1.21)	1.55 (1.13)	1.68	3.15 (1.15)	1.27 (1.16)	1.88
0.8	5.07 (1.44)	2.96 (1.29)	2.11	4.16 (1.68)	1.95 (1.41)	2.21

[a] Flux values are estimated from regression equations (see text for explanation) and are reported as geometric means (Snedecor and Cochran 1967). The parenthetical values are the 95% estimation limits which when multiplied by or divided into the flux give upper and lower estimates, respectively (Snedecor and Cochran 1967). Since J_I was derived by subtraction ($J_I = J_T - J_S$), estimation limits are not calculated

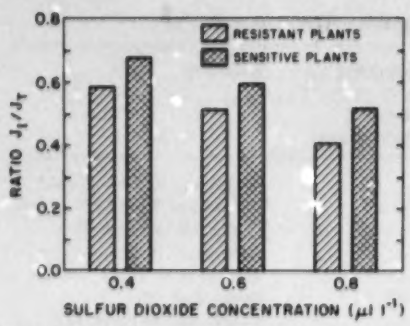

Fig. 4. Relative contribution of internal flux component (J_i) to total (J_T) flux as concentration of SO_2 increases from 0.4 to 0.8 $\mu l \cdot l^{-1}$

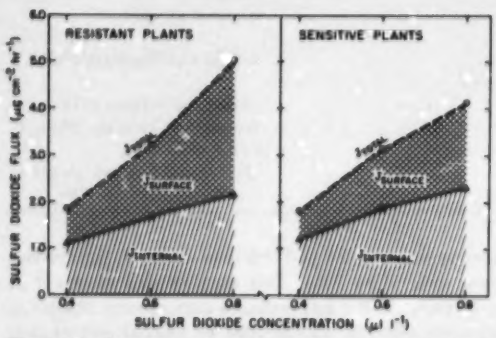

Fig. 5. Absolute values for total, surface, and internal flux fractions as a function of SO_2 concentration

50% (0.4 to 0.6 $\mu l \cdot l^{-1}$), J_i increased 51 and 55% in resistant and sensitive plants, respectively. When SO_2 increased 33% (0.6 to 0.8 $\mu l \cdot l^{-1}$), however, J_i rose only 26 and 18% for the resistant and sensitive plant groups. A similar pattern of increasing SO_2 flux is observed with J_s, but the rate of change (slope) for J_s averages roughly twice that exhibited by J_i. This difference between slopes underlies the change with concentration in relative importance of the flux fractions.

The SO_2 flux values for resistant and sensitive plants exhibit some similarities and differences. Except for J_s and J_T at 0.8 $\mu l \cdot l^{-1}$ SO_2, all corresponding pollutant fluxes at the same concentration were comparable for the two plant groups. Of particular physiological significance is the similar rates of SO_2 flux into the leaf interior (J_i). Across the range of pollutant concentrations, sensitive plants absorbed slightly more SO_2 ($\simeq$7.5%) than their resistant counterparts. This variation in J_i was not associated with differences in leaf resistance to gaseous exchange: at steady state, $R_L^{H_2O}$ was 3.50 s $cm^{-1} \pm 0.46$ and 3.54 s $cm^{-1} \pm 0.77$ ($\bar{x} \pm$S.D.) for resistant and sensitive plants, respectively.

Discussion

A notable feature of the response of vegetation to air pollution stress is variation in the extent of injury. This characteristic, common to acute and chronic responses, reflects underlying differences in plant physiology which, in turn, are a consequence of variation in either the environment or genic expression. The physiological basis of this variation is differences either in pollutant uptake into the plant or a host of subsequent physiological and biochemical processes affecting pollutant-derivative toxicity, perturbation of cell structure or function and repair mechanisms. This analysis of pollutant-leaf interactions portrays a sequence of events beginning with pollutant uptake and ending with an expression of injury. As with Levitt's dichotomy of stress avoidance and tolerance (Levitt 1972; Taylor 1978b), assessment of pollutant flux into the leaf interior is an initial step in identifying the factors underlying response variation.

SO_2 flux into the leaf interior was similar for resistant and sensitive plants although the later absorbed the pollutant at a slightly greater rate over a range of ambient concentrations. However, this difference in J_i can not be responsible totally for variation in foliar response in *G. carolinianum*. J_i values for sensitive plants at 0.6 and 0.8 $\mu l \cdot l^{-1}$ SO_2 were 1.88 and 2.21 $\mu g \cdot cm^{-2} \cdot h^{-1}$, respectively and were sufficient to elicit slight to moderate leaf necrosis. In contrast, no symptoms of leaf injury in resistant plants (with similar $R_L^{SO_2}$) were observed when J_i was 2.11 $\mu g \cdot cm^{-2} \cdot h^{-1}$. Under the experimental conditions, resistant plants did not exhibit leaf injury until the ambient SO_2 concentration exceeded 1.0 $\mu l \cdot l^{-1}$. Assuming a linear response for J_i, this would result in a J_i value of 2.6 $\mu g \cdot cm^{-2} \cdot h^{-1}$. Therefore, in order to elicit comparable levels of acute leaf injury, J_i must be 30% higher in resistant versus sensitive plants. Previous investigations (Taylor 1976) showed that diurnal leaf resistance to gaseous exchange did not differ among plants. It is concluded that genetically controlled variation in plant responses to SO_2 in *G. carolinianum* is a consequence of differences in (i) internal physiological-biochemical processes and (ii) pollutant absorption rates. The former is the predominant explanation for SO_2 response differences in this species.

The relationship between SO_2 flux and genetically controlled differences in SO_2 response has been investigated in a variety of cases, and the majority provide evidence supporting variable pollutant absorption rates as the mechanism underlying response variation (Table 2). At the inter- and intraspecific level there is no *a priori* association between pollutant susceptibility and absorption rate and, in fact, both mechanisms (variable absorption and internal physiological-biochemical processes) are reported to account for variation in SO_2 response between *Zea mays* and *Pisum sativum* (Klein et al. 1978), *Atriplex triangularis* and *A. sabulosa* (Winner and Mooney in press) and among cucurbit cultivars (Bressan et al. 1978). In the case of SO_2-induced growth rate modifications in *Lolium perenne*, Bell and Mudd (1976) concluded that variation in pollutant uptake was not responsible for disparate population responses. Conversely, in a comparison of flux rates in *L. perenne* (sensitive) and *Medicago sativa* (resistant) species, Garsed and Read (1977) reported consistently greater SO_2 uptake in the more sensitive grass.

Potential internal physiological mechanisms responsible for the differences between populations of *G. carolinianum* in their response to SO_2 are many, and pinpointing specific processes involved is difficult given the ease with which SO_2 is incorporated into existing metabolic pathways (Fried 1948 and Ziegler 1977) and the multiplicity of cellular effects (Ziegler 1975; Mudd 1976 and Malhotra and Hocking 1976). Once within the leaf interior, SO_2 may form many derivatives including SO_3^{-2}, SO_4^{-2}, HSO_3^{-2}, $SO_2 \cdot H_2O$, H^+, H_2S, free radicals and NO_2 (Ziegler 1975; Silvius et al. 1975 and 1976; Hocking and Hocking 1977; de Cormis and Bonte 1970; Klepper 1979). The importance of each in relation to acute and chronic injury is not fully resolved, however, derivatives at equivalent concentrations vary in their potential toxicity, and cellular systems may be effective in converting SO_2 from more toxic to benign forms. In this regard evidence supporting several biochemical processes is reported, including H_2S emission (de Cormis and Bonte 1970), sulfite to sulfate oxidation

Table 2. Compendium of reports addressing the physiological basis of genetically controlled variation in plant response to SO_2

Species	Variation	Differences attributed to:		Reference
		Pollutant flux	Internal biochemistry	
Populus grandidentata and *Acer saccharum*	Interspecific	×		Jensen and Kozlowski 1975
Medicago sativa and *Phaseolus vulgaris*	Interspecific	×		Garsed and Read 1977
M. sativa and *Lolium perenne*	Interspecific	×		Garsed and Read 1977
Zea mays and *Pisum sativum*	Interspecific	×	×	Klein et al. 1978
Cucurbitaces cultivars	Inter- and intraspecific	×	×	Bressan et al. 1978
Pelargonium cultivars	Inter- and intraspecific	×	×	Bonte et al. 1977
Nicotiana tabacum	Developmental	×		Craker and Starbuck 1973
Vicia faba	Developmental	×		Black and Black 1979
Lolium perenne	Intraspecific		×	Bell and Mudd 1976
Picea abies	Intraspecific		×	Grill 1972; Schindlbeck 1977
P. abies	Intraspecific	×		Braun 1977
Vitis labrusca	Intraspecific	×		Rosen et al. 1978
Arachis hypogaea, Lycopersicon esculentum, Raphanus sativus, Perilla frutescens and *Spinacia oleracea*	Interspecific	×		Kondo and Sugahara 1978
Glycine max	Intraspecific		×	Miller and Xeribos 1979
Diplacus aurantiacus and *Heteromeles arbutifolia*	Interspecific	×	×	Winner and Mooney 1980a, b
Pinus sylvestris, P. nigra and *P. pinea*	Inter- and intraspecific	×		Caput et al. 1978
Atriplex triangularis and *A. sabulosa*	Intraspecific	×	×	Winner and Mooney (in press)
Petunia hybrida	Intraspecific	×		Elkiey and Ormrod 1980

capacity (Jäger 1975; Miller and Xeribos 1979), pH buffering (Grill and Härtel 1972), glutathione balance (Schindlbeck 1977) and polyamine activity (Priebe et al. 1978). Therefore, genetically based differences in the capacity of such systems to assimilate SO_2 derivatives may be the explanation for plant-to-plant variation.

As for variation in site susceptibility within the cell as a basis for differences in SO_2 response, several mechanisms are hypothesized. Differential sensitivity of various aspects of photosynthesis are documented, including chlorophyll synthesis and degradation (Bell and Mudd 1976; Malhotra 1976), C_3 versus C_4 carboxylation reaction in vitro (Ziegler 1972), CO_2 fixation (Lüttge et al. 1972) and configuration of mesophyll tissue in C_3 and C_4 plants (Winner and Mooney in press). A more basic site of SO_2 perturbation may be cellular membranes as evidenced by early, pollutant-induced changes in osmosis (Härtel and Miklau-Grassl 1974), transmembraneous ion transport (Lüttge et al. 1972; Puckett et al. 1977), intrinsic cytoplasmic versus mitochondrial membrane associated enzyme activity (Pahlich 1973), membrane proteins (Esterbauer 1976) and thylakoidal sulfolipids (Soldatini et al. 1978). Noland and Kozlowski (1979) proposed that preferential susceptibility of membranes to SO_2 is a factor underlying rapid changes in stomatal resistance to gaseous flux. They further hypothesized that differences between and among species in their overt response to SO_2 may reflect variation in biochemical properties of guard cells that affect membrane structural and functional stability.

The response of the internal (J_i) and surface (J_s) flux fractions with increasing atmospheric SO_2 levels reveals some features of the reactivity of SO_2 with foliage. Under these experimental conditions, both J_i and J_s are quantitatively important as fractions of J_T. Each exhibits characteristics of perfect sinks since flux changes linearly with concentration. The fact that increasing pollutant levels did not affect stomatal resistance and, in turn, alter J_i is consistent with other data showing an overriding influence of humidity in controlling turgor pressure in the stomatal complex (Bonte and Louguet 1975). More SO_2 was adsorbed to the leaf surface in resistant than sensitive plants (Table 1). This is most apparent at 0.8 $\mu l \cdot l^{-1} SO_2$ in which J_s for the two plant groups differed by 34%. This suggests that chemical or structural features of the leaf surfaces vary among plants although scanning electron micrographs of adaxial and abaxial surfaces did not reveal any overt differences in morphology.

Even though J_T and J_i increase concurrently with SO_2 concentration, J_i does not change at the same rate as J_T. Furthermore, changes in the level of SO_2 in the atmosphere surrounding the plant does not necessarily effect equivalent changes in J_i. This is demonstrated between 0.6 and 0.8 $\mu l \cdot l^{-1}$ SO_2 during which SO_2 levels increased 33% and yet J_i rose only 26 and 18% in resistant and sensitive plants, respectively. Consequently, the dose to which the plant is exposed can not be used to gage accurately the amount of SO_2 entering the leaf.

The fact that plant-to-plant differences in SO_2-induced injury in *G. carolinianum* result not from pollutant exclusion but largely from differences in internal biochemistry is relevant to the process of population adaptation in *G. carolinianum*. This species is a winter annual that germinates in the fall, remains for 5–6 months as a winter rosette of 10–12 basal leaves, and then quickly flowers and fruits in the spring. Unpublished results from field studies document that plants maintain active transpiration during the winter at a rate equivalent to that during rapid spring growth. Therefore, SO_2 uptake can occur during a 5–6 month period of limited growth. If sulfur pathways and sinks become saturated with atmospherically derived sulfur, additional pollutant accumulation can have adverse physiological effect. Davies (1980) made a similar proposal to explain the greater SO_2 sensitivity of *L. perenne* during conditions of low irradiance and short photoperiod. It was hypothesized that these conditions are insufficient to provide adequate cellular reducing power to counter the buildup of sulfate and sulfite. Further attention to the potential for adverse physiological effects from polluted air during the winter has been noted for coniferous (Börtitz 1968) and deciduous trees (Keller 1978) and several grasses (Juhren et al. 1957; Ashenden 1979). In comparison with other habitat species that are more ephemeral, winter dormant or capable of rapid stomatal closure during SO_2 episodes, *G. carolinianum*

may be predisposed to accumulating greater amounts of potentially toxic SO_2 derivatives. This life cycle attribute may explain, in part, the observation that in areas experiencing frequent SO_2 exposure, *G. carolinianum* exhibited consistently the greatest extent of foliar injury among a diverse community of herbaceous species common in early seral stages of secondary succession in the southeastern United States (Taylor 1976). This same species has been used by the Tennessee Valley Authority as a sensitive indicator of SO_2 stress around SO_2-emitting facilities (McLaughlin 1972).

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